CRUSTACEAN EVOLUTIONARY EVENTS: SEQUENCES AND CONSEQUENCES

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Crustacean evolution is visualised as proceeding through a space-time continuum in which the Red Queen and stasis have operated. Under these conditions, evolutionary bursts were fuelled by major environmental changes following which the new diversities of taxa, having expanded into any newly available niches, returned to the Red Queen or stasis mode.

After some polyphyly in the Cambrian, which remains poorly understood, the major radiations in Crustacea seem to conform to such a scenario, particularly from the Hercynian tectonic epoch onwards. Important events following this include the initiation of Tethys, Carboniferous–Permian glaciations, peats and coals, Pangaea, Triassic desertic conditions, Mesozoic Tethys, the Purbeckian–Wealden, break-up of Gondwana, the Danian crisis, origin of the psychrosphere and Palaeogene Tethys, Paratethys, the Mediterranean Messinian event, the Central American filter, impingement of India against the Himalayas and of the Australian Block against the Indonesian arc, Pleistocene glaciations. Illustrations of the evolutionary effects for crustaceans are given mainly from the Ostracoda, although examples from other taxa are also cited.

Consequently, after preliminary discussion of such factors as limitations in the fossil record and convergence, new event-triggered phylogenies are derived for the main crustacean classes, maxillopodans and Ostracoda.

The role of humans in passive crustacean dispersal is analysed briefly, stressing the importance of history for a proper understanding of this phenomenon. ☐ *Biogeography, palaeontology, evolution, Crustacea, Ostracoda, man.*

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The thesis that evolution is event-triggered is well on the way to becoming a new orthodoxy in evolutionary science. Citing Benson (1985: 35), 'We are today in the middle of such a change: from the acceptance of continuity as a necessary and sufficient procedural assumption to a concurrence that interrupted stasis is an obvious condition of development.' Later in the same book Fischer (1985, fig. 7-1) correlated biotic crises with cycles of climatic change, sea level variation and vulcanism for the entire Phanerozoic (Cambrian–Recent).

There is a further modal constraint upon this paper. Van Valen (1973) propounded an evolutionary theory that all groups, 'go extinct at a rate that is constant for a given group' even in a constant physical environment. This rationale goes under the attractive name of the Red Queen hypothesis. At the court of the Red Queen extinction is inevitable, an entropic effect. Stenseth and Maynard Smith (1984) proposed an alternative hypothesis, that evolutionary stasis would be maintained until the physical environment was disturbed; then they demonstrated mathematically that both the Red Queen and stasis were feasible. This combined model is more generalised than the Macarthur-Wilson equilibrium hypothesis, in which species number is a dynamic equilibrium between immigrant taxa and those which become extinct (Webb, 1985), because it allows for the development of new taxa *in situ* following environmental change and extinction without necessitating stimulation of such evolution by immigrant competitors, although this is not excluded.

Summarising, crustacean evolution is visualised as proceeding through an Earth space-time continuum in which the Red Queen and stasis have operated. Under these conditions, evolutionary bursts were fuelled by major environmental changes after which the new diversities of taxa, having expanded into any newly available niches, returned to the Red Queen or stasis mode. The paper first briefly outlines the stratigraphy of crustacean evolution and the contemporary major environmental changes; then develops phylogenies based in the geological record; and finally cautions that passive dispersal of some crustaceans by humans can distort biogeographic (and any linked phylogenetic) patterns.

CRUSTACEAN EVOLUTION AND MAJOR ENVIRONMENTAL CHANGES

CAMBRIAN

The Cambrian Period is highly significant for the evolution of life on Earth. Although several major groups had appeared in the Ediacaran (latest Precambrian), their distribution is patchy; first appearance of widespread, richly diverse and abundant fossils is generally a diagnostic feature of Cambrian sequences. Briggs and Fortey (1989), summarising the early radiation and relationships of the major arthropodan taxa, provide a cladogram which indicates that crustaceans and crustacean-like animals occupy a primitive position among early biramian arthropodans. Their data come from the Middle Cambrian Burgess Shale fauna of British Columbia, Canada, which contains several possible crustaceans of uncertain affinities, including *Waptia*, *Odaraia*, *Branchiocaris*, *Perspicaris*, *Plenocaris* and *Canadaspis*. All were extinct by the close of the Cambrian. Boxshall (1983) also refers to the crustacean-like taxa of the Burgess Shale and includes the barnacle-like *Priscansermarinus* in his list. Confirmation that the latter is a barnacle requires the discovery and description of, 'identifiable cirriped structures, such as cirri, within the capitulum.' (Collins and Rudkin, 1981: 1011).

Canadaspis was once regarded as the earliest phyllocarid (Briggs, 1978) but this view no longer prevails and Dahl (1987) even thinks that it may not be a crustacean. Similarly, *Branchiocaris* (Briggs, 1976) seems a plausible early branchiopodan but is separated in time from more generally-accepted fossil branchiopods by about 200 million years. Briggs (1983) is unconvinced of a crustacean affinity and is similarly critical of *Waptia*, *Odaraia*, *Plenocaris* and *Perspicaris*. Note that the mandible is unknown for most of these taxa except *Canadaspis* and *Branchiocaris*, and that the *Branchiocaris* mandible is certainly non-crustacean (Briggs, 1976: 11–12).

The other Cambrian fauna with major relevance for crustacean phylogeneticists is that of the bituminous limestone Örsten of Sweden. The Phosphatocopida (Müller, 1979a), Skaracarida (Müller and Walossek, 1985) and Orstenocarida (Müller and Walossek, 1988) are all preserved in such complete detail that their assignment to Maxillopoda can be sustained. Of these taxa, Skaracarida and Orstenocarida were apparently extinct by the end of the Cambrian but Phosphatocopida lingered into the Early Ordovician and seem closely related to Bradoriida, both orders

being referrable to the Subclass Ostracoda (Maddocks, 1982; McKenzie, Müller and Gramm, 1983). Bradoriids are the commonest, most diverse and most abundant Cambrian crustaceans. They occur in Cambrian rocks almost everywhere but their geological succession and geographical distribution has been worked out most completely in China (Huo and Shu, 1985; Huo *et al.*, 1989). Huo and Shu (1983, 1985) regard naupliine bradoriids as the earliest crustacean ancestors.

The favourable environmental setting for this first evolutionary burst among crustaceans was due to the widespread marine transgression that followed a latest Precambrian glacial epoch of continental emergence. Workers on all fossil groups concur that seas were epicontinental and relatively shallow. There was also a major global climatic change from cold in the earliest Cambrian to warm in the remainder of the Period (Boucot and Gray, 1987: 33–36).

ORDOVICIAN AND SILURIAN

During the next two geological periods, the major crustacean diversifications took place among ostracodes. Maddocks (1982: 227) notes, 'This Ordovician burst of adaptive radiation of calcareous shelled types, near-simultaneous origin of the major post-Cambrian orders and rapid disappearance of Cambrian stocks is a common evolutionary pattern in many invertebrate phyla.' Thus, as Bradoriida and Phosphatocopida died out, Leperditicopida, Beyrichicopida, Podocopida, Platycopida and entomozoacean Cladocopida all evolved. The Silurian saw the initiation of the Halocyprida via Entomoconchacea (Kornicker and Sohn, 1976a). No definite Ordovician Myodocopida are known although, if the phylogeny in Kornicker and Sohn (1976b) is correct, they would have split from Cladocopida and Halocyprida before these evolved. The most characteristic Lower Palaeozoic groups, however, were Leperditicopida and Beyrichicopida. The former were an offshoot from the main lineages of ostracode evolution — their intralamellar radial carapace structures are unique within the subclass (Sohn, 1974) — and they include the largest known ostracodes (Abushik, 1979); the latter very often are spectacularly-ornamented (Kesling, 1969). Indeed, Beyrichicopida were the most abundant Ordovician (Sarv, 1972) and Silurian (Siveter, 1978) crustaceans. Their radiation during these periods was extremely complex, as the rapid evolution of numerous genera went hand in hand with almost equally numerous extinctions (Scott,

1961, figs 47, 65). Beyrichicopid systematics were long bedevilled by unrecognised homeomorphies until Scandinavian workers established the crucial importance for their classification of sex dimorphic features (Schallreuter, 1988). The role of homeomorphy in crustacean evolution is referred to again in the Discussion section of this paper.

Equally important was evolution of the first phyllocarids, beginning in the Early Ordovician with the archaeostracan *Ceratiocaris* (Rolfe, 1969). The lower Palaeozoic Archaeostraca are regarded as part of the ancestral stock of all malacostracans by some workers (Dahl, 1987).

The initiation of another maxillopodan subclass occurred during the Late Silurian. *Cyprilepus holmi,* of Estonia, was identified as a pedunculate cirriped by Wills (1963). Newman and Hessler (1989, fig. 5) derive the evolution of all Pedunculata and Sessilia from this ancestral type. Finally, F. R. Schram illustrated a Silurian remipede during his talk at the conference. This is the earliest known representative of the Remipedia.

Environmental triggers to the evolution and radiations of as many as seven ostracode orders and *Ceratiocaris* surely included the widespread tectonism of the mid-Ordovician. Seas remained epicontinental and relatively shallow and initially they were warm. There is evidence for glaciation in Arabia, northern and southern Africa, and South America, dated at near the Ordovician–Silurian boundary (Boucot and Gray, 1987, fig. 3). A good discussion is provided by Fischer (1985). This geologically short-lived global cooling indicates more varied climates at the inter period boundary and was followed by mid-Silurian tectonism.

DEVONIAN AND EARLY CARBONIFEROUS

It could be convincingly argued that this was the most important geological interval for development of the main crustacean stocks. The first shrimp-like decapods — *Palaeopalaemon* — evolved then (Sturgeon *et al.,* 1964). Other Devonian malacostracans were no less remarkable, including *Eocaris* and *Devonocaris* of uncertain affinities and the first palaeostomatopod hoplocarids (Brooks, 1969, fig. 157); also 21 genera of archaeostracan phyllocarids (Rolfe, 1969, fig. 122), such as *Echinocaris* (Sturgeon *et al.,* 1964) and *Nahecaris* (Bergstrom *et al.,* 1987).

The record for other crustacean classes was even more noteworthy. The first Branchiopoda

appeared, via the Spinicaudata and Lipostraca (note however that Schram has recently illustrated a possible Silurian anostracan). Spinicaudata are conchostracans; and they entered the geological record represented by 4 families (Tasch, 1969). Lipostraca were primitive anostracans (Scourfield, 1926). Additionally, acrothoracic barnacles evolved (*Trypetesa*).

The most abundant and diverse Devonian crustaceans, however, remained the Ostracoda, and numerous very rich faunas have been described (Pokorny, 1950; Becker and Bless, 1974; Tschigova, 1967; Jones, 1968; Polenova, 1968, 1974; Adamczak, 1968, 1976; Kesling and Chilman, 1978; Becker, 1988). While beyrichicopids still dominated, there were also many podocopids, platycopids and myodocopids; and 15 genera of leperditicopids (Abushik, 1979; Jean Berdan, per. comm. 1981) although the Order became extinct by the Carboniferous. This was also the time for diversification in entomoconchacean halocyprids (Kesling, 1954) and for the major radiation in entomozoacean cladocopids (Gruendel, 1962; Gooday, 1978).

Devonian climates are summarised in Boucot and Gray (1987: 38–43, figs 6–8) and a plausible palaeogeography is given by Rickard and Belbin (1980). Peats, red beds and marginal marine evaporites were typical on land and near the shoreline. Seas were epicontinental and mainly shallow, but reached basinal depths in regions characterised by the Thuringia-facies the most complete discussion of which is given by McKenzie (1987) who cites important prior references. The general tectonics of the Hercynian epoch are outlined by Carey (1987). Some idea of the complexity of the movements is given in the team project on the Omolon region, Siberia (Simakov *et al.,* 1983). It seems that provincialism characterised the Early Devonian whereas Late Devonian faunas were more widespread. Steiner (1967) linked the mid-Devonian biotic crisis to the dynamics of the Milky Way galaxy; for Fischer (1985) astronomical factors have neither the amplitude nor the frequency to account satisfactorily for the faunal changes which he believes were a response to a major reversal in climatic cycle, from 'greenhouse' to 'icehouse' state (Fischer, 1985, fig. 7-1). Note, however, that the tectonic setting overlapped into the Carboniferous, terminating with the definitive establishment of Tethys.

Reappraising the crustacean faunas of the Devonian, it is evident that the radiations and initiations in malacostracans (Phyllocarida, Ho-

plocarida, Decapoda), branchiopods (Spinicaudata, Lipostraca) and Ostracoda can all be explained as triggered by the mid-Devonian crisis. By its close, the Lipostraca apparently had vanished from the geological record.

On the other hand, the Early Carboniferous heralded further initiations of major crustacean groups, among them the important remipede *Tesnusocaris* (Schram and Emerson, 1986). Malacostracan initiations were primitive hoplocaridan animals (*Crangopsis*), pygocephalomorphs (*Tealliocaris, Pseudotealliocaris*), anthracocaridomorph tanaidaceans (*Anthracocaris*), primitive spelaeogriphaceans (*Acadiocaris*), as well as palaeocaridacean ancestors of the Syncarida (Brooks, 1969, fig. 157; Briggs and Clarkson, 1985; Schram *et al.*, 1986; Schram, 1984, 1988). Branchiopoda were represented by the earliest Notostraca as well as by spinicaudate conchostracans; pedunculate barnacles by *Praelepas*; ostracode initiations included cyprellid and rhombinid myodocopids, and the Darwinulacopina (Sohn, 1988).

Environments and facies of the Early Carboniferous have been exhaustively studied. The malacostracan fossils were preserved in shoreline, tidal flat, brackish-marine, deltaic and nearshore freshwater lake habitats, including coaley and apatite-rich facies (Briggs and Clarkson, 1983, 1988). Many Ostracoda also have been described from similar facies (Bless, 1973, 1983; Bless and Massa 1988; Jones 1989). Further offshore, Thuringia-type faunas persisted (Devolvé and Lethiers, 1986).

During the hot and humid climates of the time, limnic basins of thalassogenic type were widespread especially in northern continental areas. Ostracoda, in particular, were quick to exploit such niches via a number of families; typical genera included *Geisina, Carbonita, Whiplella, Darwinula* and *Tomiella* (Carbonel *et al.*, 1988, fig. 25). Their assemblages, and those of the contemporary conchostracans, were the earliest widespread continental crustacean faunas.

LATER CARBONIFEROUS, PERMIAN AND TRIASSIC

The profound changes in crustacean faunas during the later Carboniferous, Permian and Triassic were well typified by ostracodes. At the end of the Carboniferous, the following marine groups were extinct: beyrichiacean beyrichicopids; Entomozoacea and Entomoconchacea; the myodocopid families Cyprellidae, Cypridinellidae and Rhombinidae; Eridostraca; and Leperditicopida. The Permo-Triassic marine extinctions included Beyrichicopida which had dominated for most of the Palaeozoic, and also the kloedenellocopine platycopids. On land, the crisis was even more severe with only *Darwinula* and one cytheracean genus surviving into the mid-Triassic.

Other apparent victims of this series of major biotic crises were palaeocaridacean syncarids, trypetesid barnacles, *Acadiocaris*, the remipedes *Tesnusocaris* and *Cryptocaris*, and anthracocaridomorph tanaidaceans such as *Eucryptocaris*. But the lineal descendants of these taxa continued to evolve. Thus, although the earliest isopod is a Carboniferous phreatoicoid the next fossils in this group do not appear until the Jurassic.

The initiations and radiations were just as important. For Ostracoda, there were marine radiations in Bairdiacea (Kristan-Tollmann, 1970, 1971; Bolz, 1971) and Healdiacea, and evolution of the family Glorianellidae in brackish environments (Gruendel, 1978); also polycopacean cladocopids, thaumatocypridacean halocyprids and cytherellocopine platycopids (Gramm, 1968; Kornicker and Sohn, 1976a). On land, Darwinulocopina were still widespread but the faunas also included representatives of 10 non-darwinulacopine families and by, 'the end of the Late Permian, freshwater ostracode associations reached maximum species diversity and geographic differentiation for the Palaeozoic' (Carbonel *et al.*, 1988: 452).

Other crustacean initiations during the Permian included penaeid and astacid Decapoda, cumaceans, stygocaridacean syncarids (*Clarkecaris*), and perhaps the first leptostracan phyllocarids (Brooks, 1969; Rolfe, 1969; Glaessner, 1969). The Triassic was marked by the first appearances of mysids, syncaridacean syncarids, zapfellid acrothoracican barnacles, and glypheoid and eryonoid Decapoda.

Several major palaeogeographic and climatic changes were associated with these faunal developments. The continents coalesced forming Pangaea, its two main landmasses, Laurasia and Gondwana, being separated by a dominantly shallow Tethys. There was some mid-Carboniferous tectonism. Climates were glacial at higher latitudes during the Carboniferous–Permian nadir of the 'icehouse state' cycle (Fischer, 1985, fig. 7-1), but warm and humid in the tropics. During the Permian, the continents emerged and there was a salinity crisis in the mainly epicontinental seas. Towards the close of the Triassic, on the other hand, although the world

had warmed up again, climates were desertic not humid.

In marine habitats generally, ostracodes remained the dominant crustacean group in the later Carboniferous and Permian, and were excellent environmental indices in the generally shallow continental shelf seas (Melynk and Maddocks, 1988; Costanzo and Kaesler, 1987; Bless, 1987); however, Kozur (pers. comm., 1989) insists on the occurrence of some true deepwater facies (deeper than mesobathyal) in the Middle–Late Permian of Tethys.

During the Triassic, many Tethyan facies and faunas were cosmopolitan from Europe through to Asia and even the Americas (Kristan-Tollmann et al., 1987; Sohn, 1987; Kristan-Tollmann, 1988).

Niche-diversification was particularly marked on land, where brackish, freshwater and mineralised lakes were all common, each with characteristic faunas. This provided opportunities for many entrepreneurial groups, notably including syncarids and Notocostraca, although the commonest assemblages by far consisted of spinicaudate conchostracans or ostracodes. By the mid-Triassic many of these ostracodes (Carbonel et al., 1988, fig. 27) and also the vertexiid Spinicaudata (Tasch, 1969) had died out, presumably victims of the change to desertic climates. But Kazacharthra (Chen and Zhou, 1985) first appeared in the Late Triassic.

JURASSIC AND CRETACEOUS

Crustacean diversity in the Jurassic and Cretaceous was considerable in all major taxa and in all aquatic environments, continental as well as marine. Thus, in the Jurassic six more decapod superfamilies became established (Glaessner, 1969), along with numerous pedunculate barnacles (Newman, Zullo and Withers, 1969, table 2), rodgerellid Thoracica; and apseudomorph tanaidaceans. Verrucomorph, brachylepadomorph and balanomorph sessile barnacles radiated in the Late Jurassic–Early Cretaceous, but many lepadomorph genera also became extinct in the Jurassic and by the end of the Cretaceous. The Early Cretaceous saw the evolution of tanaidomorph tanaidaceans (Schram et al., 1986); and the oldest fossil copepod has been identified from the Early Cretaceous of Brazil. Ascothoracida (Endosacculus) evolved in the Late Cretaceous.

Evolutionary peaks, in what has been called the Mesozoic explosion of the ostracode Cytheracea, characterised the mid-Jurassic, mid-Cretaceous and Late Cretaceous (Whatley and Stephens, 1975). Their initiations and extinctions clearly express a Red Queen evolutionary pattern (Oertli, 1985, tables 5,6,8). Other initiations include the first Macrocyprididae (Maddocks, 1990), Sigilliacea (Szczechura and Blaszyk, 1968); and Punciacea (Herrig, 1988). The Mesozoic–Tertiary distribution via Tethys and Gondwana of entocytherid parasites is linked to the fossil history of their host taxa — phreatoicoids, cirolanids, sphaeromids, gammarideans, astacids, parastacids and potamids (McKenzie, 1973).

Continental interiors were characterised by large lake systems (including saline lakes) in tectonic depressions and intermontane basins, as in China (Chen, 1987). Darwinula and limnocytherid cytheraceans were widespread earlier, but by the Purbeckian–Wealdean epoch of alternating transgression/regression cypridaceans had taken over (Anderson, 1971; Colin and Danielopol, 1979, 1980; Ye, 1984; Su, 1987). However, most of the characteristic genera of this first continental cypridacean radiation were short-lived. With respect to conchostracans, the spinicaudate families Estheriellidae, Ipsiloniidae and Asmussiidae all died out in the Cretaceous but this was balanced by evolution of the order Laevicaudata.

World climates were in their 'greenhouse' phase according to Fischer (1985, fig. 7-1). Thus, it was generally warm to hot and humid everywhere until the close of the Cretaceous. Volcanic activity peaked in the mid-Cretaceous. High sea-levels characterised the mid-Jurassic, mid-Cretaceous and Late Cretaceous. The mid-Jurassic black marls indicate relatively deep epicontinental marine basins, with Liasina and metacope ostracodes (Oertli, 1963). Summarising the Cretaceous history of Africa, Reyment and Dingle (1987) recorded that rifting to open the South Atlantic began in the Late Jurassic but there were still connections in the Brazil–west Africa region until the mid-Cretaceous as shown by many common ostracodes (Malz, 1980). Then the break-up of Gondwana, and provincialism in the Southern Hemisphere, initiated.

Marine environments were dominated by the classic Tethys of Suess (1893) which is a mid-Mesozoic phenomenon. The analysis in McKenzie (1987) demonstrates that Tethys was not broad and uniform, as supposed by some palaeocartographers, but comprised wide continental shelves and sinuous intervening usually epibathyal deepwater facies, plus some small confined basins. It was

affected by tectono-eustatic variations in sea level which were more or less marked according as they were in or out of phase with crustal movements (Reyment and Bengtson, 1985). Thus, along the southern flank of Tethys in northern Africa and the Middle East, Jurassic–Cretaceous facies were transitional from freshwater to mineralised sabkha to brackish to shallow marine (including bituminous basinal marls) in phase with tectonism and eustasy. Ostracoda are reliable palaeoenvironmental indices (Damotte *et al.*, 1987; Majoran, 1989; Basha, 1985; Rosenfeld and Raab, 1974, 1984; Honigstein *et al.*, 1989; Al-Abdul-Razzaq and Grosdidier, 1981; Al-Furaih, 1980). The contemporary deeper-water basinal facies which covered, for example, much of France by the mid-Cretaceous (Oertli, 1985) indicate commencement of a change in Tethys, from epicontinental to truly oceanic.

The tectono-eustatic transgressions of the Cretaceous were well-marked elsewhere in the world, notably in Africa, Australia and the Americas. The characteristic crustaceans of their fossil faunas were usually ostracodes (Dingle, 1984; Kroemmelbein, 1975; Hazel and Brouwers, 1982; Bertels, 1975) or barnacles (Newman and Hessler, 1989) although many Late Cretaceous decapod-rich zones occur in the United States (Bishop, 1987).

Wholesale extinctions that devastated many groups of animals marked the Mesozoic–Cenozoic boundary. The classic study of this event has noted a major species level change in Ostracoda and the extinction of numerous marine barnacles (Kaufmann, 1985: 191); many decapod genera also died out (Glaessner, 1969, fig. 251). The environmental model proposed to account for this envisages a major eustatic sea level rise associated with active tectonism accompanied by climatic warming during the earlier Late Cretaceous, followed by sudden and widespread oxygen-depletion in the oceans and marine temperature decline during the Danian; several other possible causes are also discussed, including an extraterrestrial iridium-rich event (Kaufmann, 1985).

CENOZOIC

The Cretaceous decimations paved the way for development of the modern Crustacea. This is well brought out by the suprageneric taxa of Decapoda; Glaessner (1969, Fig. 251) shows that 32 of 51 surviving families evolved in the Tertiary–Recent. Barnacle genera with fossil records tell the same story; Newman, Zullo and Withers (1969, table 2) show that 38 of 62 genera evolved in the Tertiary–Recent, and that 27 of these were balanomorphs. For Ostracoda, the Aquitaine Basin, France (McKenzie *et al.*, 1979) has over 1100 Tertiary–Recent species; and of the more than 200 genera less than 10% have Cretaceous or earlier records.

The initiations of new major groups include 4 of the extant branchiopod orders (Fryer, 1987). There were important adaptive radiations in Copepoda, Isopoda, brachyuran Decapoda and, probably, Amphipoda. But many groups have no appreciable fossil record: including Ctenopoda, Onychopoda and Haplopoda (cladocerans); Mystacocarida; Cephalocarida; several orders of Copepoda; Branchiura; Rhizocephala; Bathynellacea; Thermosbaenacea; Euphausiacea; and Tantulocarida. This will be discussed below.

The Cenozoic also saw important extinctions, among them the rodgerellid and zapfellid Ascothoracica. Further, 26 ostracode genera had disappeared from the Aquitaine Basin by the end of the Tertiary (McKenzie *et al.*, 1979: 140).

The environmental triggers to such developments had various tectonic, eustatic and climatic components. Very important among these was the origin of the psychrosphere. The establishment of regions of abyssal and greater depths, that is the realm of true oceans, had probably begun in the mid-Cretaceous but the earliest psychrospheric ostracode assemblages have been dated as Eocene, based on Deep Sea Drilling Project cores (Benson, 1975). McKenzie (1987) considered that the ubiquity of new and specialised deep sea ostracode taxa was an indication of the comparative recency of this niche. The figures for crustaceans of the hadal zone are interesting from this point of view. Table 1 has been abstracted from Belyaev (1989). It shows that by far the largest number of crustaceans living in this deepest zone belong to comparatively young groups such as the Isopoda and Amphipoda. Even in the older groups most hadal species represent geologically young taxa, e.g. 6 ostracode Conchoeciidae (Late Cretaceous–Recent); 10 cirripede Scalpellidae, of which genera with fossil records date from the Late Cretaceous or Eocene; and 20 species of the Recent tanaidacean suborder Neotanaidomorpha (Belyaev, 1989).

During much of the Palaeogene and until the mid-Miocene, Tethys was a world-encompassing ocean in low latitudes that was psychrospheric at depth; across its entire extent

TABLE 1. Hadal Crustacea (cf. Belyaev, 1989).

Taxa	Number of Species
Calanoid Copepoda	32
Cirripedia	10 (all Scalpellidae)
Ostracoda	14 (6 Conchoecridae)
Mysidacea	12
Cumacea	11
Tanaidacea	57 (20 Neotanaidomorpha)
Isopoda	140
Amphipoda	64

ostracode assemblages contained numerous common genera (McKenzie, 1967). Tectonic pulses in the Middle East closed off western Tethys from the Indo-Pacific in the mid-Miocene. Two related events then had considerable impact upon Mediterranean faunas (Roegl and Steininger, 1984). First came the establishment of Paratethys and its sometimes linked sometimes separate component basins with their highly characteristic ostracode faunas (Pokorny, 1952; Stancheva, 1965; Sheidayeva-Kulieva, 1966; Krstic, 1971; Sokac, 1971; Yassini, 1987) which exhibited an almost 100% turnover as hasinal salinities alternated between marine, brackish and fresh in phase with tectonism and eustasy (Table 2). Destructive in a faunal sense was the Messinian (Late Miocene) crisis during which the Mediterranean dried out and thick beds of gypsum were deposited — an index for this epoch is the Paratethyan euryhaline ostracode *Cyprideis pannonica*. As a result, when the ocean refilled in the Pliocene, faunas were replaced from the Atlantic. For crustaceans, the consequences were twofold. Firstly, modern Mediterranean species have almost no links with Indopacific faunas except for a few relicts, and some Lessepsian migrants (Por, 1971) via the Suez Canal filter. Secondly, because of the Gibraltar Sill only shallow-adapted Pliocene species entered from the Atlantic, thus the Mediterranean deepwater ostracode fauna differs from that of other older oceans (Bonaduce *et al.*, 1983).

In the Indo-West Pacific, an important tectonic event was the impingement of the Australian Block against the Indonesian Arc. Unlike the earlier suturing of India with the Himalayas (which closed off a former marine corridor), this event led to faunal mixing and a new burst of marine speciation. McKenzie (1981, 1986) believes that evolution of the ostracode Subfamily Renaudcyprinae and many island assemblages in the southwest Pacific have resulted as responses to the complex Neogene regional tectonics. On the other hand, Newman (1986) ascribes the development of the barnacle fauna of the isolated Hawaiian Archipelago to long range chance dispersal during and since the Neogene.

At the western end of Tethys, a critical Neogene event was the emergence of the Isthmus of Panama which closed off the Caribbean and Gulf of Mexico from the Pacific seaboard of the Americas. Cronin (1985) and Cronin and Schmidt (1988) have discussed evolution in the ostracode genera *Puriana* and *Orionina* as an effect of this event.

On land, apart from Paratethys, large Cenozoic basins characterised by variable salinities are known from the Amazon region (Purper, 1979; Purper and Pinto, 1985) and China (Yang *et al.*, 1988). But the most important events were the glaciations of the Pleistocene Epoch. Glaciers covered much of North America, Europe and Asia wiping out all but a few relictual faunas. The reoccupation of these niches, following the last retreat of the ice sheets about 11,000 years ago, has been effected especially by parthenogenetic taxa. On other continents, endemism characterises the continental aquatic and also the terrestrial crustacean faunas. This is scarcely surprising given the long isolation of South America, south Africa, India and Australia from the northern Palaearctic and Nearctic provinces. Thus, Australia has mainly endemic faunas of anostracans, anaspidaceans, phreatoicoids, and calanoid copepods as well as ostracodes.

TABLE 2. Ostracode assemblages of the Paratethys in northwest Bulgaria (Stancheva, 1965), showing a near-complete faunal turnover in the same basin at each Stage boundary.

Stage	Total species (subspecies)	Common species with next older Stage
Pontian	47(5)	None
Maeotian	7(3)	1
Sarmatian	109(9)	2
Badenian	52(1)	-

DISCUSSION

The detail provided in the foregoing section is clearly sufficient to sustain the thesis that evolution is event-triggered. Evidently, the first evolutionary burst of Crustacea occurred in

pre-Tethyan early Palaeozoic seas; the second main episode was associated with shallow Tethys, Pangaea, and then the Laurasia and Gondwana landmasses (late Middle Devonian to Middle Cretaceous); while the third main episode relates to the evolution of deep, psychrospheric modern oceans and present continental assemblies, beginning around the middle Cretaceous (McKenzie, 1987, 1989). The data are biassed towards Ostracoda because they are the most abundant crustacean fossils. Two recent bibliographies (Kempf, 1980, 1988), both incomplete at their dates of publication by about 10% according to the author, list nearly 5100 taxonomic papers. The preponderance of these papers refer to fossil species. Numbers of described fossil Ostracoda are not known with certainty but are in any case over 30,000 and increase by several hundred species a year.

For many reasons, some of which are discussed briefly below, it is difficult to specify a typical crustacean facies. Nevertheless, the distinctiveness of the phylum is generally acknowledged. This consensus is due primarily to the work of Manton (1973) who characterised crustaceans as distinct from Chelicerata, Trilobita and Uniramia. Her assessment was vindicated on embryological grounds by Anderson (1973).

The observation has already been made that some Recent crustacean orders are not represented in the fossil record. There are a variety of reasons for this, most commonly that many groups have a wholly soft anatomy which would not be likely to fossilise except under specially favourable conditions. Other reasons include small size; unsuitable niches such as ephemeral ponds, leaf litters and caves; and inapposite habits of life such as the parasitism of rhizocephalans, branchiurans and some copepods.

Nevertheless, it is not difficult to make reasonable statements on the evolution of such taxa based on their morphology, habits and palaeobiogeography. Thus, none of the branchiopod orders once classed together as cladocerans are likely to predate the Early Cretaceous. Haplopoda (only one genus — *Leptodora*) are highly specialised marine planktic predators with a restricted Holarctic distribution (Fryer, 1987). Given that the present world ocean with its characteristic psychrosphere only initiated in the mid-Cretaceous and that there was a virtually complete turnover in oceanic plankton during the Cretaceous mass extinctions and, further, the extent of the Pleistocene ice sheets, it is unlikely

that *Leptodora* initiated much before the later Neogene. Similarly, Onychopoda are represented by few genera and although marine species are distributed worldwide the freshwater species are Holarctic. Onychopoda are also characterised by a Ponto-Caspian radiation of endemic species (Fryer, 1987). Thus, their evolution possibly correlated with that of Paratethys in the mid-Miocene. Ctenopoda and Anomopoda are certainly older and, for the latter group, fossils are known from the Oligocene and Early Cretaceous (Fryer, 1987; Jell and Duncan, 1986) — Fryer (1987) does not accept the Permian fossils described by Smirnov (1970) as anomopodans. Both groups are freshwater in origin. The numerous records of fossil freshwater ostracodes and conchostracans from every type of continental habitat make it unreasonable to claim that Ctenopoda and Anomopoda could have evolved much before the earliest accepted anomopodan fossils. Most evolutionists would agree with these conclusions since cladocerans are generally regarded as neotenic.

As further examples, the austral biogeography of the branchiuran *Dolops* and some continental calanoid copepods suggests that they probably evolved on Gondwana before it fragmented, i.e. before the mid-Cretaceous; but no phylogeny that I am aware of regards these groups as ancestral maxillopodans. Finally, but importantly, Cephalocarida (Sanders, 1963; Hessler, 1964) also have no appreciable fossil record. Their biogeography indicates wide distribution from the Americas to Asia and New Zealand, always in nearshore marine environments. This suggests that cephalocarids were dispersed via Tethys. They probably initiated prior to the mid-Cretaceous evolution of the intervening Atlantic but after the Late Devonian–Early Carboniferous, because cephalocarid fossils have not been reported from the many suitable Tethyan and other nearshore facies of this interval that would have favoured their preservation if present.

The fossil record has much more use for crustacean evolution than the simple provision of initiation times. It also demonstrates clearly that in many groups initiation is soon followed by an adaptive radiation; and as often as not a Red Queen pattern of extinctions follows this phase of diversification. Fig. 1 provides examples from barnacles, decapods and ostracodes. Further, it commonly happens in the fossil record that only one or a few taxa belonging to some particular group survive through a major biotic crisis and this survivor or survivor group

may then embark upon a new adaptive radiation or else stagnate in an evolutionary sense. The continental ostracode *Darwinula* is an excellent example. It evolved in the Carboniferous, radiated and diversified into several genera and even families by the end of the Permian, was the sole survivor of this darwinulocopine diversity after the Permo–Triassic extinctions, stagnated through the Mesozoic and most of the Cenozoic, but may now be at the threshhold of a new adaptive radiation as it is relatively species-rich and virtually euryoecious in modern continental environments and has given off the genus *Microdarwinula* (Danielopol, 1968). The fossil record also has examples of groups which became established early and have maintained a relatively limited diversity ever since. The longest surviving examples of this pattern are the Remipedia; further, the notostracans *Triops* and *Lepidurus* had split off from each other by the Triassic and have remained species-poor but persistent since then. A third pattern in the record is that in which a group initiates and then rapidly becomes extinct. A good example is provided by Kazacharthra (Late Triassic–Early Jurassic).

Very useful in the study of evolution is the principle of reductionism, termed oligomerisation by crustacean workers.

When we look, for example, at the multi-segmented and highly spinose limbs of the Cambrian maxillopodan orders Phosphatocopida, Skaracarida and Orstenocarida and compare them with the same limbs in podocopid ostracodes, cephalocarids, and copepods, the modern groups are obviously oligomerised respective to the Cambrian taxa. Exploitation of this principle, however, forms the basis of much crustacean arboriculture (to borrow D.T. Anderson's felicitous term).

On the other hand, the multiple instances of convergence (or homeomorphy) in all crustacean groups are often very difficult to deal with phylogenetically, as all workers appreciate. Less appreciated are instances of anhomeomorphy, i.e. of dissimilarities which separate taxa that in reality are monophyletic. Thus, the common characters which formerly united cladocerans now have been exposed as instances of convergence between four distinct orders (Fryer, 1987). But the anhomeomorphies between Spinicaudata and Laevicaudata (conchostracans) as elucidated by Fryer (1987) should not obscure the stem monophyletic relationship between these two branchiopod orders; the fossil record indicates that Laevicaudata split off from some Spinicaudata in the Early Cretaceous.
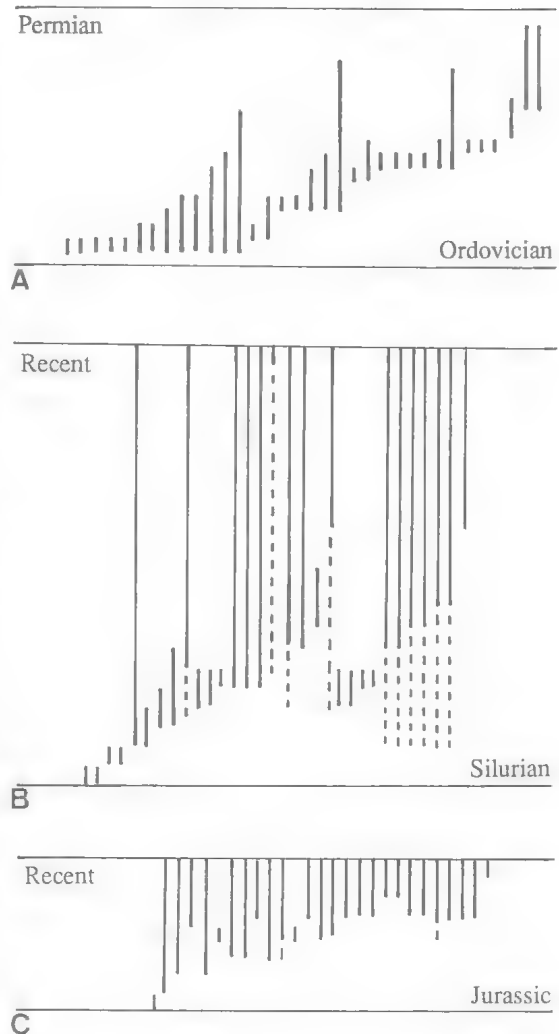

FIG. 1. A, normal radiation and Red Queen evolution/extinction in genera of Ordovician to Permian ostracodes, superfamily Drepanellacea (Scott, 1961). B, radiation, Red Queen evolution/extinction and stasis in families and genera of Silurian to Recent barnacles, Lepadomorpha (Newman *et al.*, 1969). C, radiation and stasis in families of Jurassic to Recent decapods, Brachyura (Glaessner, 1969).

Also difficult to cope with is the common occurrence of neoteny, mentioned earlier with respect to cladocerans. The recent description of a punciacean ostracode, *Manawa staceyi*, suggests that it too has several neotenic features to go with its highly-oligomerised chaetotaxy, including a shallow dome-like univalve in early ontogeny (Swanson, 1989).

A further factor which contributes to the complexity of elucidating crustacean evolution is the

frequency of mosaic evolution. This is rarely emphasised nowadays in crustacean studies although it is a characteristic phase in the evolution of numerous groups (Colin and Danielopol, 1980).

Every crustacean is a melange of primitive and derived characters. While this truth is not restricted to living taxa it leads to considerable difficulties in arriving at a plausible phylogeny on the basis solely of the Recent fauna. The problem was well aired by Dahl (1963: 13–15, figs 1,2) who warned that the main lines of phylogenies were conjectural,'for at present we possess no actual evidence demonstrating any case of a group at subclass or higher level being derived from another group.' (Dahl, 1963 : 13). The value of the punctuational equilibria hypothesis in this context lies in the fact that we would anticipate that aspect of phylogeny. On the other hand, constant reference to the fossil record enables the building of a tentative basic phylogeny that is anchored in geological time rather than in a cladistics which ignores this crucial restraint. The reasoning followed in developing a time-oriented phylogeny for Crustacea can be illustrated by reference to two fundamental crustacean characters, the carapace (or headshield) and the antennule.

There are only two arguments against the primitive nature of the crustacean cephalic shield. Firstly, some Cambrian fossils which seem to have crustacean affinities lack one, e.g. *Yohoia*. Considerable new evidence would have to be uncovered before this argument could be sustained. Thus, in Briggs and Fortey (1989, fig. 1), *Yohoia* lies between the chelicerate-like animals and the trilobites; and all the crustacean-like Cambrian fossils in their cladogram have a well-defined cephalic shield. Parenthetically, these mid-Cambrian crustacean-like taxa seem a polyphyletic cluster; their precise relationships to each other and to Crustacea remaining poorly understood. The second argument contends that Cambrian crustaceans lacking a cephalic shield have not been preserved. This argument fails because the two best known apposite Cambrian faunas, those of the Burgess Shale and the Orsten, are found in deposits that are highly-favourable to the preservation of soft anatomies: if such forms were present they surely would have been found by now. Further detailed discussion on the carapace is provided in Jones and McKenzie (1980).

My position with regard to the crustacean antennule is more controversial. Crustaceans have three types of antennule: uniramous, biramous and triramous. Uniramous antennules are typical of Maxillopoda and Branchiopoda; biramous antennules occur in the phyllocarids, eumalacostracans and Remipedia; triramous antennules feature in Hoplocarida. Kunze (1983) proposed recently that, ' Hoplocarida and Eumalacostraca evolved independently from separate "phyllocarid-like" ancestors.' The triramous hoplocarid antennule is a key apomorphy in her analysis.

Recapping, the earliest fossils assigned to Hoplocarida are Devonian palaeostomatopods. The earliest maxillopodans are Cambrian Bradoriida, Phosphatocopida, Skaracarida and Orstenocarida. The oldest-known definite phyllocarids are Ordovician, but a Cambrian origin for the group is probable. The oldest remipede has a Silurian age; the earliest Eumalacostraca are Devonian. Adaptive radiations shortly after their evolution certainly characterise the Bradoriida, Phosphatocopida, Phyllocarida and Eumalacostraca. The Skaracarida and Orstenocarida seem short-lived Cambrian groups. The Remipedia represent the pattern of a long-surviving group with limited numbers.

The simplest phylogenetic pathway that is consistent with this record suggests that the ancestral forms were Early Cambrian bradoriid maxillopodans with an uniramous antennule. Phyllocarids (biramous antennule) branched off in the mid-Cambrian, possibly from bradoriids of the suborder Abdomina (Huo and Shu, 1983). In the Devonian, Branchiopoda (uniramous antennule) split off from the Maxillopoda; but Eumalacostraca (biramous antennule) and Hoplocarida (triramous antennule) diverged separately from phyllocaridan stock (Kunze, 1983). Remipedia (biramous antennule) evolved in the Silurian or earlier, possibly from phyllocarid-like taxa. Cephalocarida (uniramous antennule) may have initiated in post-Permian Tethys as discussed previously, splitting off from as yet unknown branchiopod-like forms (Fig. 2). As a systematic exercise, it elevates Hoplocarida to the same subclass status as Eumalacostraca and Phyllocarida; but Maxillopoda, Remipedia and Branchiopoda retain their rank as classes. Note that subclass and class divergences are attuned to major Palaeozoic events.

Given this groundplan, the subdivision of classes and subclasses can proceed under similar chorological and event-triggered constraints. Remipedia are a small group whose biogeography and subsequent evolution was crucially influenced by the mid-Cretaceous separation of Africa from the Americas (Schram and Emerson,
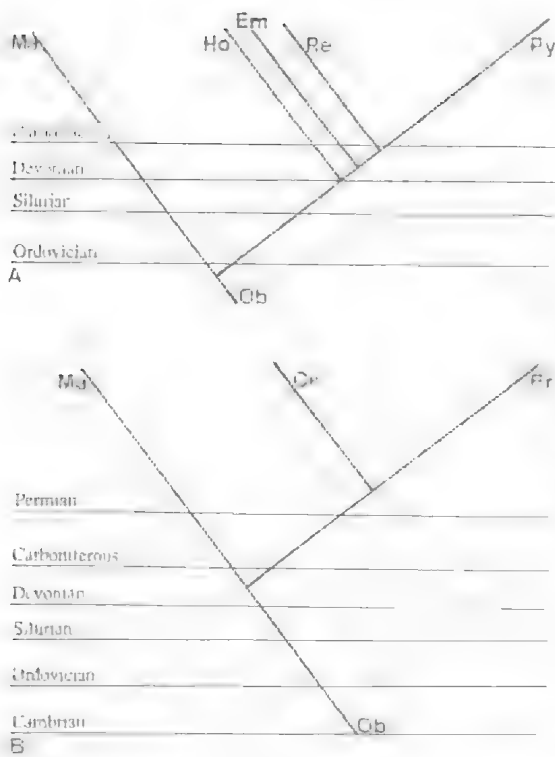
FIG. 2. A, phylogeny of Maxillopoda (Ma), Hoplocarida (Ho), Eumalacostraca (Em), Remipedia (Re) and Phyllocarida (Py) from an origin in bradoriid Ostracoda (Ob). B, phylogeny of Maxillopoda (Ma), Cephalocarida (Ce) and Branchiopoda (Br) from an origin in bradoriid Ostracoda (Ob).

1986, lower figure, p. 17). Interrelationships of the orders of Branchiopoda will be published by Fryer; but neither the evolution of Anostraca from Lipostraca, Kazacharthra from Notostraca and Laevicaudata from Spinicaudata nor the timings of these events seem much in dispute. The evolution and relationships of the families of Hoplocarida seem well understood, those of Phyllocarida and Eumalacostraca less so, but all three are beyond my expertise. This leaves Maxillopoda.

Maxillopoda were originally defined by Dahl (1956) to include Mystacocarida, Copepoda, Branchiura and Cirripedia. Later, the class was redefined to include also Ostracoda, Tantulocarida and the Cambrian orders Skaracarida and Orstenocarida (Grygier, 1987; Boxshall and Huys, 1989; Müller and Walossek, 1988). The two latter orders, with Bradoriida and Phosphatocopida (Ostracoda), serve to emphasise the early adaptive radiation of maxillopodans and

the equally important subsequent early extinctions.

Thanks to painstaking work by Müller (1979a, 1982) and Müller and Walossek (1985, 1988), the anatomies of Phosphatocopida, Skaracarida and Orstenocarida are known in considerable detail. A comparison indicates clearly that the most generalised limbs are those of the phosphatocopid suborder Vestrogothiina in which the antennule is reduced (*Falites*), the antenna through to the maxilla are biramous and closely similar in morphology, the 6th and 7th limbs are modified from the antenna-maxilla pattern and the 8th 'limb' is lamellar (possibly a furca). In Hesslandonina, the antennule is small and uniramous, antenna and mandible are biramous and similar, and the maxillule, maxilla, 6th and 7th limbs while differing somewhat from the antenna-mandible pattern are also similar (Müller, 1979a, 1982).

The organisation of Skaracarida limbs resembles that of Hesslandonina, i.e. uniramous antenule, look-alike antenna and mandible, similar maxillule, maxilla and maxilliped; but the rest of the body is strikingly distinctive comprising 10 circular limbless segments, followed by a telson and 3-segmented furcae (Müller and Walossek, 1985).

Bredocaris, the representative of Orstenocarida, has differentiated anterior limbs, comprising uniramous antennule, biramous antenna, mandible with well defined coxal gnathobase, maxillule; but the maxilla and 7 thoracopods are similar to each other. The body ends in a short abdomen and furcae (Müller and Walossek, 1988).

The earliest fossils of these maxillopodan orders are Early Cambrian naupliine Bradoriida, the most primitive of which (*Shensiella*) seems to have possessed four body segments not including the telson, indicated by lobe-like expansions of the soft and very thin outer surface of the carapace shield (Huo and Shu, 1983: 87). The progressive decrease in lobes through stratigraphically higher beds indicates fusion of the body segments terminating in an unsegmented body (*Hanchungella*). This ancestral stock then divides into the Lipabdomina (lacking an abdomen) and Abdomina (with an abdomen). Jones and McKenzie (1980) also suggested such a division in Bradoriida but regarded it as evidence for polyphyly. However, the discovery of Naupliinae substantiates a monophyletic origin for the order.
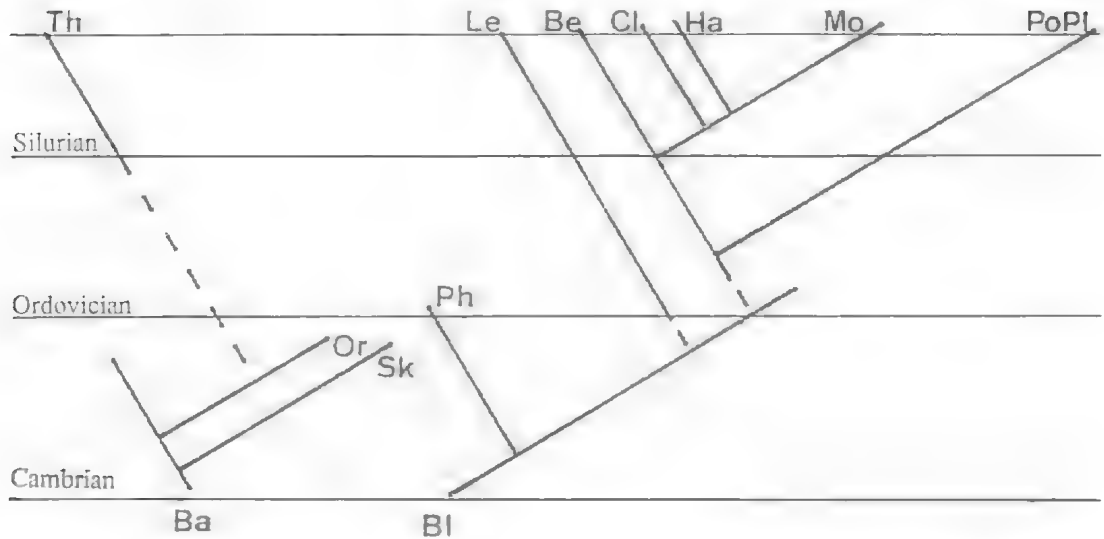
Fig. 3 presents phylogenies of the early Max-

FIG. 3. Phylogenies of the maxillopodan orders and the superorder Thecostraca. Left hand side shows the phylogeny of Skaracarida (Sk), Oerstenocarida (Or) and Thecostraca (Th) from an origin in bradoriid Abdomina. Right hand side shows the phylogeny of the ostracode orders Phosphatocopida (Ph), Leperditicopida (Le), Beyrichicopida (Be), Cladocopida (Cl), Halocyprida (Ha). Myodocopida (Mo) and Podocopida/Platycopida (PoPl) from an origin in bradoriid Lipabdomina..

illopoda based on an origin in naupliine Bradoriida. On the left, the orders Skaracarida and Orstenocarida split successively from Abdomina; and Thecostraca are interpreted as diverging from Orstenocarida (Müller and Walossek, 1988). On this main branch, Tantulocarida evolved subsequently from thecostracans (Boxshall and Lincoln, 1987); Branchiura also from Thecostraca; Copepoda from Skaracarida-like forms; and Mystacocarida from Copepoda (Boxshall and Huys, 1989, fig. 6).

Copepod specialists will decide whether or not the Early Cretaceous parasitic species from Brazil is close to the ancestral Copepoda. Based on geological history, copepods probably diversified nearshore and on land after the Triassic; profited from the mid-Cretaceous opening of the Atlantic; were exposed to Cretaceous decimation; and underwent an adaptive radiation especially in the oceans during the Cenozoic. Mystacocarida, with their interstitial and cavernicole life habits and longitudinal distribution from Europe to southern Africa, probably evolved from copepod ancestors during the opening of the Atlantic. A possible geological history for some Branchiura was given earlier.

The right hand side of Fig. 3 provides a phylogeny based on Lipabdomina and shows evolution of the ostracode orders. Phosphatocopida diverged via Oepikalutidae (Jones and McKenzie, 1980) in the Midddle Cambrian; Beyrichicopida in the Late Cambrian possibly via Beyrichonidae (McKenzie, Müller and Gramm, 1983); Leperditicopida perhaps in the Late Cambrian (Scott, 1961). Podocopida branched off from Beyrichicopida in the Early Ordovician, and Platycopida possibly from Podocopida in the Late Ordovician; while Myodocopida evolved from Beyrichicopida in the Ordovician, giving rise to Cladocopida and Halocyprida in the Ordovician and Silurian respectively, as discussed earlier. The cladistics of the three latter groups is based mostly on Kornicker and Sohn (1976b). Kornicker (pers. comm., 1981) accepts the ordinal status of Cladocopida. Lastly, the photograph of an *Amphissites* soft anatomy in Müller (1979b) shows that a beyrichicopid origin for podocopids and platycopids is plausible.

EPILOGUE

History is the biostratigraphy of *Homo sapiens*, now self-recognised as a rather insensitive dominant in the organic world. A main feature of this dominance has been the passive dispersal of thousands of species, usually deliberate but also, on numerous occasions, accidental. Thus, ever since the first human settlements people have transformed their sur-

rounding environments by the cultivation of exotic but useful plants. The earliest such introductions can be dated archaeoethnobotanically, but most information on the spread of useful plants is accessed by studying socio-economic history.

Many crustaceans have minute dessication-resistant eggs that could be transported easily with seeds of exotic cereals and other plants, in soil packed around cuttings; also as dust carried with trade goods, and by travellers and migrating peoples. Both archaeoethnobotanical and historical records were cited by McKenzie and Moroni (1986) in documenting the role of humans as an agent of crustacean passive dispersal via useful plants with respect to the many ostracode *ospiti esteri* (foreign guests) of northern Italian ricefields. These species originated variously, in Africa, Australia, Asia and South America. None of them have been identified in European Tertiary and Quaternary fossil assemblages. The authors also stressed that numerous other exotic plants could have been the first vectors for such introductions (McKenzie and Moroni, 1986). Margaritora, Ferrari and Crosetti (1987) found a Far East *Moina* (cladoceran) in an Italian ricefield which they thought came in with seed exchanges; and Ferrari (pers. comm., 1989) has identified an Oriental calanoid copepod in northern Italy.

Marine Crustacea are also susceptible to passive dispersal by humans, the principal vector in this instance being shipping ballast. The earliest ballasts were large stones — clumps of ballast stones can still be seen on atolls, such as Aldabra in the Indian Ocean — and the mud and water associated with these could harbour small crustaceans. Thus the homogeneity of shallow water ostracode assemblages in island groups of Micronesia (Weissleader *et al.*, 1989) may well be due in part to passive dispersal via frequent inter-island voyages.

Sea trade was well established even before Roman times and by the 12th century Islam controlled the Asian sea routes. With the Chinese invention of bulkheads (Needham, 1971), large ships capable of long oceanic voyages could be built. The Ming admiral Zhung He established a Chinese hegemony in the Indian Ocean early in the 15th century, but this lapsed when later Ming emperors adopted an isolationist policy. In 1492, Columbus discovered America and in 1493 Vasco da Gama sailed round southern Africa to India. Soon Portugal, Spain, Holland, France and Britain were colonising and trading directly in Asia and the Americas. When needed, ballast was dredged up by shipboard pumps from harbour bottoms. This practice continues and now poses a serious quarantine problem worldwide. For example, around 60 million tonnes of ballast water are discharged in Australian waters each year; and crustaceans are known to be among the numerous organisms dispersed internationally in this way (Australian Quarantine and Inspection Service pamphlet, 1990). My own research has concentrated upon trade in the Mediterranean for which the historical records are excellent, particularly those in the Venetian archives (Borelli, 1985). Maddocks (pers. comm., 1988) has suggested that some unexpected ostracode distributions off Florida may be due to passive dispersal in the ballast of pirate ships during the 16th to 18th centuries.

Many discontinuous distributions of Recent crustacean species and genera are simply explained by passive dispersal in ballast sludge during the past 500 years. Apart from taxa cited in McKenzie (1989), the ostracodes *Mungava* and *Dolerocypria* (Wouters, 1987a, 1987b) and the harpacticoid *Darcythompsonia* (Fiers, 1986) could have been distributed passively in such a manner.

Obviously, any taxa spread by humans on land or by sea are allochthonous to the geological evolution of Crustacea; and phylogenetic interpretations based upon such distributions are faulty. Because crustacean taxonomy itself is only about 250 years old many of these dispersals predate it; but others, particularly of small species, are still occurring.

ACKNOWLEDGEMENTS

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